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ON THE HABITS AND REACTIONS OF SAGARTIA DAVISI.

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Sagartia davisi[1] is the Pacific representative of the *S. luciæ* of the Atlantic coast of the United States. The two species appear to differ only in the absence, in *S. davisi*, of the narrow yellow stripes on the column which are so characteristic of the eastern form. Both species commonly reproduce by fission, and it is probable that the following descriptions of some of the other habits of *S. davisi* may be applicable to *S. luciæ* also.

S. davisi was first discovered clustered on the valves of a species of the bivalve *Chione*, common in the harbor of San Pedro, Cal.[2] The clam dwells near or on the surface of the sand. As it plows its way along, the uppermost regions of the shell are about the hinge and the siphons. To these regions, invariably, the polyps cling. The deeper the clam goes the more do their small, thin-walled bodies lengthen, supported by the surrounding sand, to a degree I have never seen in an erect and unsupported form. *S. davisi* is not, however, a burrower, nor is the association with *Chione* a case of commensalism, as might be concluded at first sight. It fastens readily to any object which can give it a foothold and keep it out of the sand. On the sand flats at San Pedro

[1] Description. Column of largest polyps about 1 cm. in diameter; spread of tentacles about 2 cm. Foot disk very extensible; body wall everywhere quite thin and semitransparent; a distinct capitulum above a well-defined collar as in *Metridium;* oral disk almost circular, mouth small, oval, lips with about twelve lobes, not prominent; one or two, occasionally three siphonoglyphs. Tentacles tapering, slender, pointed, variable in number, most often 45–50 in perfect individuals. Color of column dark brown, tentacles and disk green. Many individuals with light longitudinal stripe of variable width on column (zone of regeneration after fission). Mesenteries unusually variable in number and arrangement. Reproduction sexual and non-sexual; latter the cause of irregularities in number and arrangement of tentacles and mesenteries.

[2] It has since been found in San Diego Bay, Cal.

it was uncovered about half each day by the falling of the tide, during which periods its tentacles were completely retracted, contrary to the custom of such typical sand dwellers as *Harenactis attenuata*,[1] and another species of *Sagartia* from San Pedro as yet undescribed. It may live permanently submerged, however, and thrives in aquaria.

Though ordinarily attached to a solid substratum, it is occasionally found free on the sand. Its powers of locomotion are considerable. By means of multicellular amœboid processes of the foot disk, readily seen with a hand lens at the edge of the disk, it is capable of creeping more than an inch in an hour. The polyps often leave the clam to which they are attached when placed in an aquarium, especially when they are on the lower valve. They may occasionally creep along the surface of the water, hanging from the surface film.

The inverted position is not long retained, however, for *S. davisi* has a marked tendency to assume as erect a posture as its situation will permit. An example of this tendency is provided in the case just mentioned, of the relatively greater haste of the polyps in leaving the lower than the upper valve of a clam lying on the aquarium floor. Moreover, the axes of polyps clinging to the vertical sides of the aquarium are either perpendicular to the sides or bent upward. They never bend downward if the polyps are submerged.

The orientation of *S. davisi* is, then, partly a result of geotropic stimulation. The same may be said of the locomotion of the species. There is a definite tendency of the polyps on the walls of the aquaria to collect near the surface, although the aquaria may be sealed jars completely filled with water, or furnished with green water plants evenly distributed (precautions against the possible influence of oxygen at the surface). The polyps on the floor of the aquarium, if it be horizontal, move about but little, and when they do, sporadically and without certainty of direction. When by chance, however, they reach the angle made by the floor and a side of the aquarium and begin an ascent, there is never a retrograde movement, seldom a halt, until they draw near the surface. This locomotor geotropism is especially inter-

[1] Torrey, 1901.

esting from the fact that the major axis of the animal is not parallel with the direction of locomotion, a peculiarity which distinguishes it from the reactions of the majority of animals to directive stimuli. The major axis is the axis of geotropic orientation, but it can only be the axis of locomotion in swimming forms [1] and those which lack a foot disk and creep on the column (*e. g.*, *Peachia*).

It is possible to reconcile these different cases if we think of the foot disk merely as a differentiated portion of the body wall. *Edwardsia* has no well defined foot, though its aboral end is rounded and adhesive. The hydroid, *Corymorpha*, again, has no foot such as is possessed by *Hydra*, its aboral end coming to a point; yet the sides of this tapering extremity are adherent, and through their amœboid cells the hydroid, orienting negatively to gravity, tends also to move vertically upward. It adheres in this case by a portion of what may truly be called its lateral wall; in consequence of which the axes of locomotion and geotropic orientation coincide. *S. davisi* is an extreme case in the other direction. Having a large and well defined foot, it can hardly be said to cling obviously by a portion of the lateral (*i. e.*, column) wall. At the same time, when on a vertical surface, its axes of locomotion and orientation are as nearly parallel as the differentiation of foot and column will allow. This, however, is not equivalent to saying that the direction of locomotion in response to a directive stimulus is determined by the orientation of the major axis of the polyp, for the elements of the foot may be directly affected by gravity.

Loeb ('91, p. 70) has said that *Cerianthus* and *Actinia equina* went from smooth glass to a mussel shell or piece of ulva more readily than in the reverse direction in his experiments. This indicates a certain "contact irritability," which seems to be possessed also by *S. davisi*, as the latter moves about more freely on smooth glass than on rough surfaces. The reaction to the contact stimulus, however, is not so strong as the orienting re-

[1] Besides the pelagic species which Andres describes among the *Minyadidæ*, all non-adherent, there is an interesting polyp abundant in the harbor of Honolulu which, I am told by my friend Mr. Loye H. Miller, leads both a sedentary and a free existence. It appears to have no pedal float, sustaining itself by means of rhythmic movements of the tentacles which send it along foot foremost at a fair rate of speed.

action in response to the stimulus of gravity, so that as a resultant of the opposing responses, the polyp leaves the shell for the glass as stated above.

Light does not appear to stimulate *S. davisi* in any way. The polyps neither bend nor move toward the light when it comes from but one side of the aquarium, in all degrees up to the intensity of bright daylight. Neither do flashes of sunlight falling upon polyps in a darkened aquarium produce any muscular responses. *S. davisi* differs in this respect from *Cerianthus membranaceus* and *Edwardsia lucifuga*, according to Nagel ('94, p. 545).

The responses of anemones to mechanical and chemical stimuli have been investigated already by Pollock ('82), Loeb ('91 and '95), Nagel ('92, '94*a*, '94*b*) and Parker ('96). With most of the conclusions of these investigators my own observations accord. I must differ with some, adding also a few facts which to my knowledge, have not been published heretofore.

Two quite distinct reactions usually follow the stimulation of a tentacle of *S. davisi* by means of a slight touch with a needle or glass rod. The first is a bend at and toward the point of stimulation, whether the latter be near tip or base, on right side or left, above or below, and appears to be due to the response of the muscles involved to a direct stimulus. The second is a contraction of the whole tentacle, with a simultaneous bending of the tentacle toward the mouth. Evidently all the longitudinal muscles of the tentacle not previously active are indirectly excited to produce this reaction, those on the inner (upper) side between base and point stimulated contracting more strongly than the outer (lower) muscles. This unequal contraction is probably to be explained by the greater strength of the inner muscles, which play the greater part in the chief work of the tentacles — carrying food to the mouth. The hydroid *Corymorpha* shows this inequality still more strikingly; the first reaction of *S. davisi* is entirely wanting and the outer muscles are in use only when the tentacles are slowly returning to their expanded condition after a contraction. But I have been unable to demonstrate histologically any difference in size between outer and inner muscles, in either animal.

The result of the second reaction is varied. Often the tentacle merely waves stiffly inward. At other times it may arch so that its point is directed toward the mouth. On the whole, however, its movements are less definitely adaptive than those which Parker describes for *Metridium*.

The second reaction does not always follow the first. The general contraction does not appear to be induced by contact alone. If the tentacle be touched lightly and for but an instant, only the first reaction occurs. If, however, the stimulating object rest against the tentacle sufficiently long to allow the latter to adhere to it, the second reaction immediately follows. Whether this results from the adhesion itself, or the duration of the stimulus, or a tension in the muscles due to the resistance of the stimulating object, I am unable fully to decide. Such small objects are capable of producing this reaction that the third possibility seems to be excluded. Whichever of the other two be the efficient stimulus, it produces a strong contraction of the muscles directly affected. This strong contraction probably serves as a direct stimulus for contiguous muscles, the contraction of these for others, and so on, until all are involved. In no case did the evidence enforce the assumption of the presence of nerves, in the tentacular responses.

So far the movements of but a single tentacle have been considered, without relation to the others. And it should be said here that tentacles cut from the polyp behave in all essential respects as they do under normal circumstances. Often the stimulus applied to one tentacle is sufficient, unless care be used, to induce contractions in several. It may be that only a few tentacles on each side of the one touched will react; with a stronger stimulus the entire set of tentacles may contract with vigor. There is no more evidence, however, that this correlation of parts is attained by the aid of nervous tissue than there was in the case of the single tentacles. Communication from one tentacle to the next is largely through the oral disk. The proper degree of contraction of a tentacle induces a contraction in neighboring muscles in the oral disk, and possibly in contiguous tentacles directly. The vigor of the stimulus, if it be local, appears to determine the extent of the

response, which spreads by the direct effect of the tension of one muscle on those near it.

The usual response of a tentacle stimulated indirectly in the manner just described is a waving or arching toward the mouth, with or without vigorous shortening of the whole tentacle. Occasionally the response is quite opposite to this, the stimulation of one tentacle producing an outward waving of neighboring tentacles. The anomaly is only apparent, not real, for as a matter of fact the muscles of the neighboring tentacles are not involved at all in the latter case. The tentacles neither shorten nor bend. They move outward stiffly, owing to a local contraction of muscles in the oral disk or the capitulum.

If the stimulus applied to a tentacle be sufficiently strong, all of the tentacles may shorten simultaneously, may even be entirely withdrawn into the body by the contraction of mesenterial muscles and hidden by the contraction of the sphincter; the column may shorten also, and the foot disk may change its shape. All of these movements seem to be induced by the direct passage of the stimulus from muscle to muscle without the aid of nerve tissue.

The oral disk, between tentacles and mouth, is almost insensible to mechanical stimuli.

Stimuli applied to the column produce the inward movement of several or all tentacles, the outward movement of a few, or the contraction of column and foot disk, according to the strength of the stimulus. Stimulation of the foot disk, either at the edge or on the lower surface, produces local contraction of the foot and base of the column, and acontia are usually emitted near the point stimulated. The tentacles may contract also, but always as a whole, the same general reaction following stimulation at different points of the disk instead of a local reaction as in the cases of the foot, column and acontia. This inability of the tentacles to recognize the direction of the stimulus is also characteristic of the reaction of the tentacles of *Corymorpha* to stimulation of the column, and is due, I believe, to the opportunities for diffusion of the stimulation impulse owing to the distance of the reacting structures from the point at which the stimulus is applied.

The entire surface of *S. davisi*, with the possible exception of

a small zone between mouth and tentacles, responds to a mechanical stimulation, the greatest irritability being manifested by the tentacles, the tactile organs *par excellence.* The latter exhibit a very definite adaptive reaction. The preliminary bend of an irritated tentacle at and toward the point stimulated makes it possible for the polyp in a sense to pursue its prey actively if, indeed, to but a limited extent. The great advantage of this reaction over the simple inward movement of the tentacle indirectly stimulated is obvious. The latter is also adaptive, however, since it is the most likely movement to clutch food organisms in a polyp whose tentacles are habitually outstretched. Supporting this idea is the fact that the tentacles of hydroids react only in this way, whether stimulated directly or indirectly. It is the simpler, more primitive reaction.

A more efficient adaptive reaction, also indirectly induced, is the extrusion of acontia at the point stimulated, for purposes of defense. Though the reaction is always the same, the acontia always move in the most desirable direction, which is not always the case with tentacles.

The passive outward movement of tentacles due to the contraction of muscles in the oral disk or capitulum is not directed by the position of the stimulating object. It may be toward the latter, but only when the stimulus happens to be applied at a point external to the tentacles, that is, at some point which is less likely to be stimulated by a food organism than points on their inner surface. When a tentacle of an outer whorl is moved passively as a result of the stimulation of a tentacle of an inner whorl, the movement is away from, not toward the tentacle stimulated. The reaction in this direction is of no obvious importance to the polyp in this case, and seems to be of no more importance, in the sum of all cases, than a movement in any direction. It appears, therefore, to have no adaptive value whatever.

By means of its varying sensitiveness to different chemical substances and its ability to discriminate between mechanical and chemical stimuli, *S. davisi* is enabled to make certain choices in its quest for food. This capacity, which it possesses in common with other anemones, has been described as olfactory by Romanes

and Nagel, and as gustatory by Jourdain. Such expressions, however, are essentially psychological, and Loeb ('91) has justly insisted upon the substitution for them of some physiological expression, such as *chemical irritability*. This power of discrimination has been shown by Loeb to reside not only in the tentacles (Nagel, '92), but also in other regions. *Actinia equina* discriminated between crab's flesh and small rolls of paper as definitely after he had removed the tentacles by a transverse cut as before. Parker ('96) demonstrated later that *Metridium dianthus* reacts in different ways to mechanical and chemical stimuli.

Actinia equina, from Loeb's observations, is so definite in its choices that chemically inert paper pellets were never taken into the mouth. Parker found that *Metridium* would swallow pieces of white india rubber as well as flesh, though the former were sometimes disgorged before they had passed out of the œsophagus. Since he has shown that the cilia covering the lips of *Metridium* and beating outward in the absence of chemical stimuli, reverse their dominant beat in response to the stimulation of meat juices, their behavior when stimulated by apparently chemically inert india rubber leaves a doubt as to whether or not they can be reversed by purely mechanical means. There is, however, no doubt of such a reaction in *S. davisi*, as will be shown in the course of the following account of my experiments.

It may be well to begin with the effects of various chemicals. Cane sugar in solutions of various strengths produced no appreciable reactions in any part of the polyps on trial. Strong picric acid and 4 per cent. formalin caused the retraction of all the tentacles, indicating stimulation of body muscles. One half per cent. hydrochloric acid caused a general contraction of tentacles. From a knowledge of the behavior of *Corymorpha*, which, though unable to detect the presence of flesh until touched by it, yet reacts strongly to strong alcohol and acetic acid, I am led to suspect that these substances irritate the polyp in the same way that they irritate one's skin, through the tactile organs merely.

Crab's muscle, bits of limpet and annelid worm were used as

stimulators with uniform results. Small amphipods were devoured with avidity. The response differed according as the stimulus was applied locally or generally. For my first experiment I placed a small piece of worm on several of the outstretched tentacles of a polyp. The tentacles immediately adhered, bending at and toward the point stimulated, as though responding to a purely mechanical stimulus, and then contracted, dragging the morsel to the mouth. For some seconds the tentacles not in contact with it remained motionless. Then, one or two at a time, they waved slowly inward and grasped the flesh, almost every tentacle finally becoming thus engaged. This experiment was tried many times with similar results. Apparently the tentacles not mechanically stimulated were irritated by substances in solution diffusing out of the flesh, and the reaction was as definite as it would have been if induced by a mechanical stimulus. The movement was toward the stimulus.

The possibility of an indirect stimulation of these tentacles through the oral disk from the tentacles touching the flesh was eliminated by holding a piece of worm flesh immediately above the mouth of another polyp. In a few seconds some of the tentacles began to twitch slightly, and a little later all began to wave slowly inward, toward the flesh, finally grasping it. A similar result followed numerous trials.

Next, a bit of flesh was placed on the aquarium floor, near, but not in contact with the foot disk of another polyp. Would the tentacles bend in the direction of the flesh now, or toward the mouth? This experiment, repeated a number of times, did not give uniform results. In the majority of cases the tentacles waved toward the mouth, *away from* the flesh. In the rest they moved *toward* the flesh in the most definite and unmistakable manner. Not only that; the column, in several cases, bent toward the morsel which was seized by the tentacles nearest it and dragged toward the mouth. There is no doubt here that the movements were in the direction of the stimulating object, and are thus comparable to the well-known movements of the manubria of various mendusæ toward stimulated points on the subumbrella. The proboscis of *Corymorpha* reacts similarly, as will be shown in a forthcoming paper.

Pollock ('82) observed this fact but was unable to reconcile his varying results. The reason for his failure was, I believe, that he failed to distinguish between *general* and *local* stimulation. When the meat juices of the annelid used previously were discharged gently over a polyp from a pipette, I observed that the tentacles always waved inward, without regard for the direction from which the juice was coming. This general chemical stimulation produced the same response from the tentacles that a mechanical stimulation of the foot disk provoked. In both cases then, in which the tentacles waved inward and away from the flesh, the diffusion of soluble substances from the latter was probably so rapid that the tentacles were stimulated *on all sides* so nearly at the same time that no differential of stimulation beween opposite sides of the tentacles was established, the necessary condition of a directive reaction. But why the movement toward the mouth? Because it is the primitive clutching movement already spoken of as most likely to capture food organisms, in a polyp whose tentacles are habitually outstretched. It is the simplest adaptation of the prehensile mechanism, common to hydroids as well.

The responses of the tentacles to mechanical and chemical stimuli are essentially the same. The bend is toward the stimulus when the stimulation is local, toward the mouth when it is general, whether direct or indirect.

If we turn now to the phenomena of swallowing, we shall see that the cilia of both lips and œsophagus may respond to mechanical as well as chemical stimulation by waving more strongly inward than outward. I early observed that not only were pieces of flesh occasionally rejected, but bits of shell and gravel were sometimes taken in. With the idea in mind that the size and shape of the object might affect the reaction, several substances, presumably chemically inert, were given to various polyps, in pieces varying in these respects. Pieces of very thin paper, from 1 mm. to 3 mm. square, when placed npon the tentacles, were cast off in half an hour. A piece of cork, about one fourth as large as the polyp, was likewise rejected. A much smaller piece, capable of being easily ingested, was taken into the gullet and retained for thirty minutes. A piece of paraffine of similar

size was swallowed in three minutes, and a half-cube of heavy drawing paper, of about the same size, was also swallowed, though more slowly. Tiny bits of glass were frequently swallowed.

I can say definitely that these objects were not carried in by the beat of the cilia covering the siphonoglyphs and producing an insetting current, but by cilia covering the lips and œsophagus between the siphonoglyphs and producing a current which ordinarily sets outward. It would seem, then, that chemically inert substances, if small enough to be taken easily into the mouth and thus brought into direct contact with the ciliated cells lining the œsophagus, are ingested under some conditions. Other experiments show that one of these conditions, probably the most important, is the degree of hunger of the polyp. Starving polyps were always more ready than well fed individuals to swallow chemically inert substances. Some explanation of this fact may be derived from the further fact that hungry polyps are in general unusually sensitive to both chemical and mechanical stimuli. Increased sensitiveness means increased effectiveness of a given stimulus ; this is equivalent to saying that the stimulus is more intense. *S. davisi*, then, responds only to certain intensities of the same stimulus, so far as the ciliated cells of the lips and œsophagus are concerned. Under mechanical stimulation of a given intensity, the cilia do not reverse their beat ; an increase in the intensity or, if you will, effectiveness of the stimulation may produce this reversal. To chemical stimuli, or to mechanical which are above a certain degree of intensity (*i. e.*, when the stimuli polyp is starving), the response is usually positive ; to a weakened mechanical stimulus there is less likelihood of any response.

The positive response to mechanical stimuli is undoubtedly advantageous to the polyp. It is apparent that substances with even a very small food value must be of some importance to a starving polyp although they would not be desirable as food for a well nourished animal. For the latter they would come into the category of useless substances, which the ciliary currents on œsophagus, lips and tentacles are admirably adapted to remove.

The disgorgement of non-nutritious bodies may now be briefly considered. All harmless non-nutritious bodies, and all food stuffs from which the nutrient juices have been taken during the process of digestion, are sooner or later cast out of the mouth. The cause of the ejection is to be found in the behavior, under varying stimulation, of the œsophageal cilia. The mesenterial filaments bordering the mesenteries, and the defensive filamentous acontia, are ciliated, but probably take no part in the process, for several reasons.[1]

First, the mesenterial filaments pursue excessively meandering courses along the edges of the mesenteries, and their cilia produce many currents which are antagonistic instead of proceeding in one general direction. I have not been able to determine whether the cilia beat more strongly away from or toward the mouth. In all parts of each filament, however, they appear to beat in the same direction ; and this beat is not reversed by contact with meat or meat juices. Second, the cilia on the acontia beat always more strongly toward their free ends, and they too do not reverse their beat in the presence of meat juices. Since the acontia are attached by one end only, have a marked tendency to coil, and occupy without regularity of arrangement any position in the cœlenteron, they can hardly be concerned with the phenomena of disgorgement. It may be noted in passing, however, that when they are thrust through mouth or cinclides, their cilia, in carrying toward their tips whatever foreign particles may come in contact with them, are performing what must be in the long run an advantageous service.

Finally, the œsophagus itself, ordinarily more than half the length of the column, reaches nearer to the foot disk when the polyp contracts as it does with food substances within it. The objects taken into the cœlenteron never get far away from the lower edge of the œsophagus. Under the influence of the mesenterial and acontial cilia, they may, if small enough, rotate aimlessly about during the period of digestion and absorption. In the absence of direct stimulation, the œsophageal cilia resume

[1] The following facts concerning the behavior of the cilia on mesenterial filaments and acontia were obtained from *Metridium*, but I feel confident that the same results would have followed an investigation of *S. davisi* had the supply of material permitted.

their dominant outward beat, and are able to carry away non-stimulating objects. At the end of the period of digestion and absorption, the ingested bodies have reached their minimum of stimulating power; and now, no longer able to reverse the dominant beat of the œsophageal cilia, they are carried out by the latter just as soon as they come into their sphere of influence. Why chemically inert bodies, once swallowed, should be disgorged, may be explained, I believe, by assuming inability on the part of the œsophageal cilia to continue reversing their dominant beat in the presence of a persistent or frequently applied mechanical stimulus which was originally weakly positive. This is in entire harmony with Parker's demonstration that after repeated applications of a weak chemical stimulus to the lips of *Metridium*, there comes a time when no positive reaction results.

Peristaltic movements of the œsophagus may assist the cilia, but I have no evidence that they take more than a very subordinate part in the phenomena of swallowing or disgorgement.

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